

THE ENIGMATIC GENUS *PYTHIELLA* (OOMYCOTA)

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ABSTRACT

Pythiella (Oomycetes, Stramenopiles) is a small genus of hyperparasitic organisms (parasitic in other parasitic Oomycetes). These obscure organisms may escape notice, and are probably more common than reports suggest. *Pythiella* and its original species, *P. vernalis*, are technically nomenclaturally invalid; no Latin diagnoses were provided with original descriptions (Couch, 1935). Biological validity of organisms identified as *Pythiella* should, though, be further established before effecting nomenclatural validity. Four putative species of *Pythiella* are known, although the most recently described of these has not been named. These taxa exhibit a similar, achlyoid (“ball-like”) mode of spore discharge; sporangia are illustrated herein. The history of *Pythiella* is reviewed in hope of fostering interest in these puzzling organisms. A key to species is presented—a preliminary guide, given the relatively meager systematic information available to this point. *Phytologia* 92(3) 304-311 (December 1, 2010).

KEY WORDS: *Achlya*, biflagellate, cysts, *Ectrogella*, *Glaucocystis*, holocarpic, *Olpidiopsis*, oogonium, *Pythium*, *Spirogyra*, zoospores.

Pythiella species are poorly known Oomycetes—difficult to find, not obtainable from culture collections, tedious to manipulate (not yet cultured without hosts); they are holocarpic (the thallus completely converted to asexual or sexual reproductive structures). Sequence data and ultrastructural information are lacking. However, enough details of morphology are known—knowledge admittedly mixed with an array of questions—that it is possible to offer a taxonomic synopsis. Zoospore behavior—systematically significant among Oomycetes (cf. Powell and Blackwell, 1998; Blackwell and Powell, 2000)—appears to unify the genus. Perhaps this presentation will promote additional discoveries of the life cycles of organisms assigned to *Pythiella*.

TAXONOMIC HISTORY OF *PYTHIELLA*

In 1935, Couch described *Pythiella* (lacking Latin diagnosis), a genus seemingly combining features of several oomycete genera: *Olpidiopsis*, *Aphanomycoopsis*, *Pythium*, *Ectrogella*, *Achlya* and *Saprolegnia*. *Pythiella* was of further interest in that it parasitized hyphae of *Pythium* (*P. gracile* and *P. dictyosporum*) which in turn parasitized filaments of *Spirogyra*. Microscopically obvious swellings or “galls” in threads of *Pythium* contained *Pythiella*—either a spherical sporangium (Fig. 1) with sometimes elongate, occasionally branched exit tubes, or a single-spored oogonium with an antheridium attached by a small fertilization tube (Fig. 5). The mode of spore discharge, in which internally cleaved spores aggregate, externally, in a ball-like cluster of primary cysts—at or near the opening of a sporangial discharge tube—reminded Couch of the saprolegniaceous genus, *Achlya*. Secondary, swarming, biflagellate zoospores developed from the primary cysts. A single species exhibiting these sporangial and oogonial features, *Pythiella vernalis* (also lacking Latin diagnosis), was recognized by Couch. As the only original species of *Pythiella* (Couch, 1935), *P. vernalis* is the type of the genus; Couch reported depositing preserved slide material at the University of North Carolina Herbarium. Among oomycete genera, Couch believed *Pythiella* to have its closest relationships to *Ectrogella* and *Aphanomycoopsis*, despite certain differences in appearance of the protoplasm (cf. Couch, p. 167).

Sparrow (1943) initially considered *Pythiella* somewhat similar to *Olpidiopsis*, and placed it in the Lagenidiales (Oomycetes). Sparrow and Ellison (1949) described a parasite of *Olpidiopsis schenkiana* (itself a parasite of *Spirogyra*), found in Michigan, which they named *Ectrogella besseyi*. Sparrow and Ellison indicated that Scherffel (1925) and Domján (1936) had (wittingly or not) figured an organism recognizable as *Ectrogella besseyi* in drawings of *Olpidiopsis* (see, for example, Domján, Fig. 173). Although possessing a more asymmetric thallus (Fig. 2)—sometimes lobed or tubular (in some cases more than one thallus being present in an old *Olpidiopsis* cell)—Sparrow and Ellison (1949) mentioned a resemblance of certain other features (e.g., an achlyoid mode of spore discharge) of *E. besseyi* to Couch’s *Pythiella vernalis*. Sparrow (1960) later became convinced of a closer relationship of *E. besseyi* to *Pythiella* than to *Ectrogella*, and effected

transfer of this species, viz. *Pythiella besseyi* (Sparrow & Ellison) Sparrow. In considering Orders of Oomycetes, Sparrow (1960) concluded that *Pythiella*—given its zoospore behavior, and a general relationship to *Ectrogella*—had its connections with the Saprolegniales rather than the Lagenidiales. Unfortunately, details of sexual reproduction of *Pythiella besseyi* remain unobserved, leaving the relationship of this organism still somewhat in question.

Whiffen (1946) described an *Olpidiopsis*-like species of *Lagenidium*, *L. pythii*, found in *Pythium* sp., growing on grass-leaf bait in a water culture of a soil sample from Cuba. Several spherical or flask-like sporangia (Fig. 3)—each with a single, short, relatively stout exit tube—were observed in club-like swellings of the *Pythium* host; other swellings contained oogonia or resting spores; in some instances, sporangia and resting spores occurred in the same swelling. Whiffen noted that spore discharge in *L. pythii* was anomalous for *Lagenidium* [being more similar to *Achlya*]; nonetheless, Whiffen placed this organism in *Lagenidium*. Sparrow (1960) and Karling (1981) continued to recognize this *Pythium* parasite as a species of *Lagenidium*. However, Dick (2001, p. 245, 337) concluded that *Pythiella* should include this taxon. The combination *Pythiella pythii* (Whiffen) Dick should date from Dick (2001, p. 337)—not Dick (1998), as Dick (2001, p. 245) appeared to imply. *Index Fungorum* and *Index Nominum Genericorum* correctly cite Dick (2001) for the combination *Pythiella pythii*.

Dick (2001, p. 244-245) considered *Pythiella* a genus “Insertae Sedis,” and stated that *Pythiella* (i.e., the type species, *P. vernalis*)—though definitely an oomycete, with laterally biflagellate zoospores—“does not have unequivocal affinity” to any particular known oomycete order. Dick doubted the biological authenticity of *Pythiella besseyi*, considering its alleged occurrence an example of “autoparasitism” by *Olpidiopsis schenkiana*. Dick (2001, p. 337) excluded *Pythiella besseyi* from *Pythiella*. However, illustrations by Sparrow and Ellison (1949) and Domján (1936)—and my observations of what was apparently this organism in *Olpidiopsis* occurring in *Spirogyra* in central Alabama—suggest not only that *Pythiella besseyi* exists, but that its morphology is distinctive from *Olpidiopsis*. As a further point of confusion, Dick (2001, p. 245, 337) stated that he placed this organism (*Pythiella*

besseyi) in *Pleocystidium*, and is credited with the combination (*Pleocystidium besseyi*) in *Index Nominum Genericorum*; this combination is also listed, minus authorship, in *Index Fungorum*. Dick (2001), though, did not make this combination under *Pleocystidium* (p. 345-346), or in his discussion on p. 245. Dick (p. 345) was apparently merely suggesting that *Olpidiopsis schenkiana* be included in the synonymy of *Pleocystidium* (under *P. parasiticum*). Dick (2001) did list the combination “*Pleocystidium besseyi* (F. K. Sparrow & B. Ellison) M. W. Dick” on p. 337; however, this does not seem to be where the combination was effected; in the index of his book Dick refers (this combination) to p. 236, but it does not appear on this page.

It is difficult to know how common *Pythiella* is, as it surely often goes unnoticed as an inconspicuous parasite of other oomycete parasites (even these are not always readily detected). Czeżuga (1991) reported *Pythiella vernalis* from a lake in Poland. Pires-Zottarelli et al. (2009) documented *Pythiella vernalis* in Brazil, in a different *Pythium* host (*P. aphanidermatum*) than previously reported. Kühn and Schnepf (2002) reported “*Pythiella* sp.” parasitizing a *Lagenidium* parasitic in *Glaucocystis nostochinearum* from a freshwater pond in northern Germany. This unnamed *Pythiella*—relatively smaller than *P. vernalis* (the species mainly compared by Kühn and Schnepf)—is not identical in sporangial morphology to other taxa of *Pythiella*, being often ovoid and possessing a more slender, irregular, discharge tube (Fig. 4); this tube is not branched (as it sometimes is in *P. vernalis*), and multiple tubes (per sporangium) do not occur (as they often do, for example, in *P. besseyi*). In spite of differences, achlyoid spore discharge was observed. Primary zoospores of this *Pythiella*, described by Kühn and Schnepf, very briefly exhibit flagella before encysting; typical swarming, laterally biflagellate secondary zoospores are then observed. In other *Pythiella* species, only one flagellated stage is seen, i.e., the equivalent of the secondary zoospore stage; a primary cyst stage was, however, illustrated for *P. vernalis* by Couch (1935).

GENERIC DESCRIPTION, KEY TO SPECIES

Below is quoted the original generic description of *Pythiella*, given by Couch (1935) in English but not Latin. Since the rule (Article 36.1, ICBN, 2006) requiring a Latin description or diagnosis took effect

January 1, 1935, *Pythiella* is (by “the letter of the law”) an invalid name, as is the species name, *P. vernalis*. Should *Pythiella* prove to be a biologically viable genus, it will require nomenclatural validation, even if current attempts to repeal the “Latin Rule” succeed (cf. Figueiredo et al., 2010); i.e., such a change would not be retroactive. Following Couch’s description, I present a preliminary key to the four supposed species of *Pythiella*, including *Pythiella* sp. (Kühn and Schnepf, 2002).

Description of *Pythiella* by Couch, 1935

“Plant body parasitic within the threads of *Pythium*; without rhizoids, the entire thallus upon maturity being transformed into reproductive organs. Spore development as in the higher water fungi (*Achlya* and *Saprolegnia*, e.g.). Spores after emergence encysting at the tip of the sporangium as in *Achlya*, swarming later in the laterally biciliate condition. Antheridia present on all oögonia. Egg not completely filling the oögonium, and with a distinct periplasm.”

Preliminary Key to Species of *Pythiella*

- 1. Occurring in *Pythium*. Sporangium generally spherical or flask-shaped; discharge tube branched or unbranched.
 - 2. *Pythium* host parasitic in *Spirogyra*. Sporangium typically one per host “gall” or swelling, occasionally more; discharge tubes may be more than one per sporangium, often longer than sporangium, somewhat irregular, sometimes branched.....*Pythiella vernalis* Couch, 1935
 - 2. *Pythium* host occurring on vegetable matter, not in *Spirogyra*. Typically more than one sporangium found in host “gall;” discharge tube one per sporangium, shorter than sporangium, stout and regular, unbranched.....*Pythiella pythii* (Whiffen) Dick, 2001
- 1. Occurring in hosts other than *Pythium*. Sporangium shape variable, often ovoid or asymmetric; discharge tube unbranched.
 - 3. In *Olpidiopsis*, which in turn occurs in *Spirogyra*. Sporangium 13-

42µm, often somewhat asymmetric, sometimes tubular or lobed; discharge tubes often more than one per sporangium, usually less than sporangial length, more or less regular; one motile zoospore stage.....*Pythiella besseyi* (Sparrow & Ellison) Sparrow, 1960

3. In *Lagenidium*, in turn found in *Glaucocystis*. Sporangium 12-17 µm, ovoid to spheroid; discharge tube slender, irregular, often becoming greater than sporangial length, only one present per sporangium; primary zoospores (briefly) and secondary zoospores developing flagella.....*Pythiella* sp.
(described but unnamed, Kühn and Schnepf, 2002)

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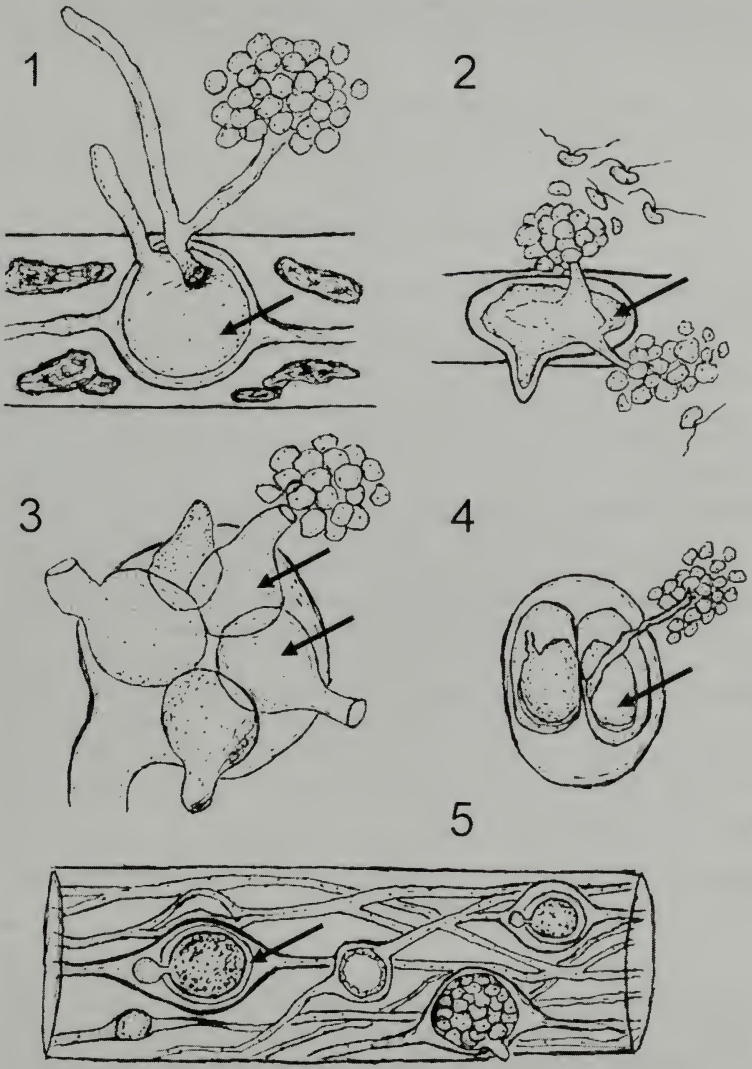
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Fig. 1 (based on Couch, 1935): Sporangium (arrow) of *Pythiella vernalis*, in swollen area of *Pythium* hypha (in *Spirogyra*, plastid remnants evident). **Fig. 2** (after Sparrow and Ellison, 1949): Sporangium of *Pythiella besseyi* (arrow) in old *Olpidiopsis* cell (in *Spirogyra*). **Fig. 3** (after Whiffen, 1946): Sporangia (arrows) of *Pythiella pythii*, in *Pythium*. **Fig. 4** (based on Kühn and Schnepf, 2002): Sporangium (arrow) of *Pythiella* sp. in *Lagenidium* (in *Glaucocystis*). **Fig. 5** (based on Couch, 1935): *Pythium* hyphae (in *Spirogyra*); “gall” with oogonium (arrow) of *Pythiella vernalis*; antheridium attached (opposite arrow). Another gall (to right) shows cleaved primary spores.



Figures 1-5, see caption on previous page.